



Research Paper

Local and global climatic drivers of Atlantic salmon decline in southern Europe

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ABSTRACT

The abundance of Atlantic salmon is declining throughout its geographical area. Fisheries and global warming were assumed as main drivers of the decline, and recent studies suggest that habitat changes in freshwater is a third contributor. Southern populations experience the greatest decline, and face the highest risk of extinction as global warming moves its thermal niche northwards. We analysed long-term catch data (1949–2013) from a salmon fishery in northern Spain, and examined its relationship with local and global indicators of temperature and hydrological change. CPUE data, analysed by ARIMA time-series models, exhibited a significant negative trend and a marked decrease since 1973–1974, possibly triggered by overfishing at sea and a sudden outbreak of disease. Temperature increased in the same period, particularly so since 1986–1988, being negatively correlated with CPUE. A significant change in magnitude and duration of extreme water conditions occurred from 1970s onwards. Indicators of hydrological shift were also significantly correlated with CPUE of returning salmon. The best ARIMAX models indicated however, that the decrease in salmon CPUE was mainly driven by temperature trends. This indicates that both local (temperature and flow in the river) and global (ocean temperature) factors have contributed to the decrease in salmon numbers, and that temperature has played the major role. Despite a strong reduction in fishing pressure after the 1970s widespread collapse, our study population did not recover to previous abundance levels. This suggests the operation of additional factors, being climate warming and changes in food webs of the North Atlantic the most likely reasons.

1. Introduction

Climate is important for nearly all aspects of life on earth. For instance, it influences species abundance, geographical distribution and behaviour as well as interspecific interactions in food webs (Van der Putten et al., 2010). Thus, with climate change, the ecology of species varies, and predictions on species responses to climate change strongly rely on projecting altered environmental conditions on species distributions and abundances.

One species that has exhibited a dramatic decrease in abundance during recent years is Atlantic salmon *Salmo salar* (Chaput, 2012; Mills et al., 2013; Friedland et al., 2014). The total reported nominal catch has fallen by ca. 90% in 40 years from ca. 10,000 tons in the early 1970s to ca. 1000 tons in recent years (ICES, 2013). The consistency in the global trend, in spite of variation in smolt production, suggests that factors influencing survival and growth at sea most likely are

responsible for a large part of the decline in North America and Europe (Friedland et al., 2003; Jonsson and Jonsson, 2004). The decreased marine survival has been attributed to overexploitation, global warming and decreased zooplankton abundance in the North Atlantic (e.g. Potter et al., 2004; Todd et al., 2008; Beaugrand and Reid, 2012), but in several cases, local conditions are blamed (Vøllestad et al., 2009; Otero et al., 2011). The variable explanations may be because Atlantic salmon exploit freshwater, estuarine and oceanic habitats, and factors affecting their survival in all these environments influence population abundances. Possibly, the influence of factors in freshwater may be greater than previously assumed (Otero et al., 2011), and that fluctuating conditions in freshwater may be a key to the future viability of the species, particularly in southern populations in Europe and North America (Friedland et al., 2009; Jonsson and Jonsson, 2017).

Climate change is expected to have a negative effect on early life stages of salmon in freshwater (Jonsson and Jonsson, 2009; Todd et al.,

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2011). The fish is thermally sensitive and oxygen demanding and requires cold, clean water (Elliott and Elliott, 2010), and is highly sensitive to extremes in flow (Jonsson and Jonsson, 2011). These variables control the smolt production, migration pattern and survival during downstream migration (Jonsson, 1991; Juanes et al., 2004; Jonsson and Jonsson, 2017). Furthermore, water flow influences opportunities for feeding and spawning (Hvidsten et al., 2015), stimulates smolt migration, and mark the time of ascent when returning from sea (Tetzlaff et al., 2008). Later at sea, warm surface water may have detrimental effects on growth and survival (Mills, 2000; Friedland et al., 2005; Todd et al., 2008). An additional negative effect appears caused by decreased abundance of pelagic food items and increased competition from other zooplanktivores in the North Atlantic (Beaugrand and Reid, 2012; Jonsson et al., 2016a).

Jonsson and Jonsson (2009) pointed out that the ongoing decline in Atlantic salmon abundance is most pronounced in the southern distribution areas of salmon, but information from these areas in Europe is scarce. In North America, southern populations appear subjected to increased predation and ocean warming (Hogan and Friedland, 2010; Friedland et al., 2012; Hansen et al., 2012). The southern range limit has been reduced by 2° latitude, and the remaining southern stocks are critically endangered (Juanes et al., 2004; Mills et al., 2013). A report from ICES (2013) shows that the catches in traditional fishing areas of Irish, British, French and Spanish populations have fallen radically and the return rates of multi-sea-winter (MSW) salmon have particularly decreased. Possibly, the decline is caused by reduced growth and survival at sea associated with warmer marine conditions and decreased marine feeding opportunities, as well as decreased smolt production because of increased flow variation in rivers (Beaugrand and Reid, 2012; Piou and Prévost, 2013; Friedland et al., 2014).

Processes and causes of the decline in Spanish salmon are unclear, mainly because most of the salmon's life in the ocean is unknown. There are almost no data on the migration of Spanish salmon, as there has been no tagging programme. The few available records suggest that Spanish salmon occupy similar feeding areas as British, Irish and French salmon, at west Greenland and north of the Faroe Islands (Jacobsen et al., 2012; Reddin et al., 2012). Because lack of knowledge prevents a consistent management policy, it is important to identify the historic and current factors that have influenced the decline of the species. Managers should use the evolutionary potential of the species to deal with climate change, and this includes the conservation of the southernmost populations. The Iberian Peninsula was a glacial refuge of the species during the Pleistocene glaciations (Consuegra et al., 2002; Finnegan et al., 2013), and with a possible loss of these populations, a valuable part of the genetic variability of the species may disappear.

Here, we investigated how the abundance of Atlantic salmon in a river in northern Spain has varied with climate from 1949 to 2013, and analysed its relationship with local and global indicators of temperature and hydrological change over these 65 years. We hypothesised that the population abundance was driven by both local and global variables, and predicted that climate, as a determinant of flow and water temperature, shapes salmon abundance.

2. Materials and methods

2.1. Study area

The River Sella (43°28'N, 5°03'W), at an altitude ranging from zero to 1100 m in northern Spain, is probably the most important salmon river in Iberia (Fig. 1). The river is 66 km long, total drainage area is 1284 km². The river is accessible for upstream migration of Atlantic salmon and is not affected by land use change, pollution or flow regulation. The water quality is within the limits set by the European Directive (Council Directive 2006/44/EC).

The River Sella was declared a Site of Community Importance (Code ES1200032) under the European Commission Habitats Directive (92/

43/EEC), and it contributes significantly to the conservation of freshwater habitats within the Natura 2000 network of protection areas in the European Union. Most other South-European fresh waters have been historically subjected to strong human pressures, so the interaction of multiple human stressors hinders the interpretations of the natural changes suffered by salmon populations. Therefore, this study is a good opportunity to assess the natural changes responsible for the development of salmon populations in a river almost free of human stressors.

The regional climate is oceanic, with profuse precipitations and mild temperatures year around. The annual mean temperature and precipitation within the study area are close to 15 °C and 775 mm, respectively. The analysis of the regional climate over the past decades (1970–2010) shows a slight decline in annual precipitation and a clear increase in temperature, especially during spring and summer (González-Taboada and Anadón, 2011). The projections for air temperature and precipitation in the study area under the representative concentration pathways RCP 4.5, 6 and 8.5 (Van Vuuren et al., 2011) show a similar trend, although with projected harsher conditions in autumn and a slight acceleration of the process after 2040. In the future, spring, summer and autumn will be hotter (an increase of up to 5 °C in both maximum and minimum summer temperatures) and dryer (a decrease of up to 25% in mean autumn precipitation), whereas the effect of climate change is expected to be lower in winter.

2.2. Salmon abundance

We analysed 65 years (1949–2013) of returning adult salmon captured annually from March to July. Catch per unit effort (CPUE) from recreational salmon fisheries were used as an indicator of abundance. The CPUE has traditionally been a proxy of abundance in salmon studies, because long-term data of density were not available (Rand et al., 2012). Nowadays, there is enough evidence that CPUE reflects changes in the population size of returning, migrant Atlantic salmon (cf. Vøllestad et al., 2009; Mills et al., 2013; Friedland et al., 2014). Local management authorities have regularly collected these data since 1949. This is the only measure of abundance that has been collected over time. The number of fishing licenses in the study area has not changed significantly with time (Mann-Kendall test corrected to account for temporal autocorrelation, $\tau = -0.036$, $p = 0.68$). Therefore, it is reasonable to assume that the fishing effort has remained stable over this period. Moreover, there was no significant relationship (analysed through both simple and lagged regressions) between number of fishing licenses and the catch of salmon.

2.3. Climate indicators

We analysed the long-term trend in land-ocean temperature anomalies (°C) for Europe and the Northern Hemisphere through three different climate indicators. We used datasets from the NASA Goddard Institute for Space Studies (GISS indicator, GISTEMP Team 2016 <http://data.giss.nasa.gov/gistemp/>, Hansen et al., 2010), the NOAA National Climatic Data Centre (NCDC indicator, <https://www.ncdc.noaa.gov/cdo-web>, Smith et al., 2008), and the UK Meteorological Office Hadley Centre-University of East Anglia Climatic Research Unit (HadCRUT indicator, <http://www.metoffice.gov.uk/hadobs/hadcrut4>, Jones et al., 2012). These global climate indicators combine records from sea surface temperature and air temperature from local meteorological stations. The three approaches use the same input observations, but handle the data differently (Hansen et al., 2010).

The term 'temperature anomaly' denotes the difference between a reference average value from a 'pre-industrial' period from 1850 to 1899 and the current temperature. Positive anomalies indicate that the current temperatures are warmer than the reference values, while negative anomalies indicate that they are colder. This indicator has been measured for several decades in a dense network of stations across the

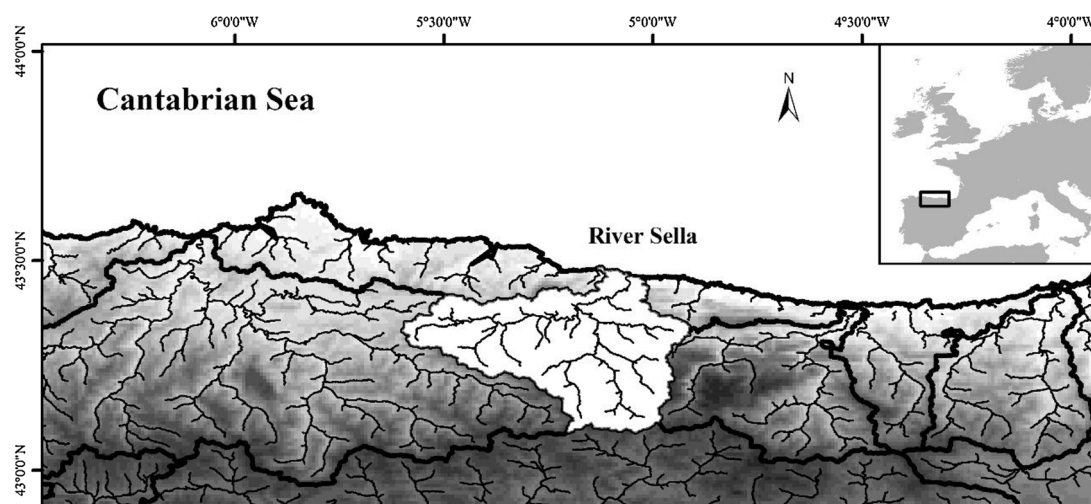


Fig. 1. Map of the study area.

world and gives one of the clearest and most consistent signals of global and regional climate change.

Local climate change was assessed by analysing the temporal trend of surface temperature anomalies in the study area. Data were obtained from the ENSEMBLES daily gridded observational dataset for surface temperature in Europe (E-OBS v. 13.1, <http://www.ecad.eu/download/ensembles/ensembles.php>, E-OBS indicator, Haylock et al., 2008). This is a high-resolution daily land dataset using the European Climate Assessment and blended daily station datasets (ECA & D). We averaged the data from the $0.25^\circ \times 0.25^\circ$ grid cells that cover the whole basin of the River Sella. The temperature anomalies were calculated as the difference between the long-term average temperature (reference value, 1950–2013) and the current temperature. Thus, the long-term average temperature is the expected temperature, and the anomaly is the difference between the expected and the current temperature.

The available time series of water temperature in the River Sella, collected by the Spanish Ministry of Environment, covers a shorter period than land surface temperature anomalies, from 1980 to 2011. The time series was not long enough to perform a rigorous trend analysis; nevertheless, it was used to analyse the relationship of water temperature with the local climate indicator during the period of available records, and assumes that this relationship would hold for the entire study period (1949–2013).

2.4. Flow indicators

We estimated ten indicators of flow variation based on data from River Sella, collected by the Spanish Ministry of Environment. The gauging station was located close to the monitoring sites. Daily discharge data from 1949 to 2013 were processed by IHA 7.1 software (The Nature Conservancy, 2011). We estimated mean annual flow (Mean), the magnitude and duration of extreme water flow, measured as the minimum and maximum discharge during seven (7Dmin and 7Dmax) and 30 consecutive days (30Dmin and 30Dmax) recorded each year; and the number and duration of high (HpF and HpD) and low (LpF and LpD) flow pulses within each year. High and low flow pulses were defined as periods when the daily discharge rose above the 75th percentile or dropped below the 25th percentile of all values each year. Rates of change in discharge were measured dividing the hydrologic record into “rising” and “falling” periods that corresponded to periods in which the respective daily changes in flows were either positive or negative. The annual number of reversals (Rev) is the number of times that flow switches from one type of period to another.

2.5. Data analyses

We used the non-parametric Mann-Kendall test modified by Yue and Wang (2004) to identify significant trends in CPUE and environmental indicators each year. Breaks in non-homogeneous time series were determined by the Pettit homogeneity test (Pettit, 1979; Hipel and McLeod, 1994). Significances were estimated by Monte Carlo permutation tests (10^4 permutations).

CPUE data (1949–2013) were analysed by time-series models to determine their autocorrelation structure. Model identification techniques were used to select the time-series model that best characterised the autocorrelations among the observed data, to identify a model that effectively explained patterns and interdependences in the observations (Brockwell and Davis, 1996; Shumway and Stoffer, 2000). Time-series models were classified as autoregressive, moving average, or autoregressive integrated moving average (ARIMA) (Box and Jenkins, 1976). Two criteria, the adjusted R^2 and the Bayesian Information Criterion (BIC), were used to select the most appropriate, parsimonious models. Both criteria are performance measures that balance model fit and model parsimony. The Expert Modeller features in the SPSS version 23.0 were used to automatically determine the best-fitting ARIMA model. An interrupted time-series design (i.e., a time-series analysis in which the series is divided or interrupted by the intervention into two periods, pre-intervention and post-intervention, which were compared), based on the models developed by McDowall et al. (1980), was used to examine the temporal trend in salmon abundance. Prior to the analysis, salmon abundance was subjected to the Jarque-Bera test of normality (Jarque and Bera, 1980). Data were log-transformed before the analysis to meet the normality assumption. The autocorrelation of residuals from ARIMA models was assessed by applying the Ljung-Box test (Ljung and Box, 1978).

The relationships between CPUE and the environmental indicators were first evaluated with Spearman's Rank-order correlation analysis. We then fitted an autoregressive integrated moving average model including exogenous covariates (ARIMAX) to the CPUE time-series. ARIMAX is an extension of an ARIMA model that includes the linear effect that one or more exogenous time-series has on the response time-series. Here, we used the best autocorrelation structure identified in the previous analysis and added only the climate and flow indicators that were significantly correlated to salmon CPUE as exogenous predictors, after removing variables that were highly correlated between them (Pearson's $R > 0.8$). We tested all possible combinations of exogenous predictors (128) and chose the model with the lowest value of the Akaike Information Criterion corrected for small samples (AICc).

All statistical analyses were performed using SPSS version 23.0

Table 1

Results of the trend analyses (Mann-Kendall tau τ , positive trend $\uparrow$, negative trend $\downarrow$), and homogeneity tests (Pettit statistic K, break year in brackets) for local (E-OBS) and global (HadCRUT, GISS, NCDC) indicators of temperature anomalies and hydrologic alteration (7Dmin, 30Dmin, 7Dmax, 30Dmax, LpF, Rev) in the River Sella during the period 1949–2013. See Material and Methods for more details. All tests were significant at $p < 0.0001$. The table also includes the results of pairwise correlations (Spearman tests, R and p) between temperature and flow variables and Atlantic salmon CPUE.

	Mann-Kendall (τ)	Pettit (K)	R	p
HadCRUT	0.39 ($\uparrow$)	825 (1987–1988)	−0.517	< 0.0001
GISS	0.44 ($\uparrow$)	862 (1987–1988)	−0.561	< 0.0001
NCDC	0.43 ($\uparrow$)	844 (1987–1988)	−0.551	< 0.0001
E-OBS	0.36 ($\uparrow$)	774 (1986–1987)	−0.433	< 0.0001
7Dmin	−0.56 ($\downarrow$)	852 (1979–1980)	0.367	0.003
30Dmin	−0.47 ($\downarrow$)	782 (1979–1980)	0.316	0.012
7Dmax	0.35 ($\uparrow$)	718 (1974–1975)	−0.336	0.007
30Dmax	0.39 ($\uparrow$)	780 (1971–1972)	−0.363	0.003
LpF	0.33 ($\uparrow$)	660 (1981–1982)	−0.354	0.004
Rev	0.44 ($\uparrow$)	926 (1981–1982)	−0.390	0.002

statistical software (SPSS Inc., Chicago, Illinois), but the *forecast* package for R v8.0 (Hyndman et al., 2017) was used to fit the ARIMAX models. The analysis was performed in R 3.3.3 (R Core Team 2017).

3. Results

3.1. Climate and water flow indicators

The climate variables used for assessing trends in the Northern Hemisphere and European land-ocean temperature anomalies were highly correlated (range $R = 0.817$ – 0.993 ; $p < 0.0001$, $n = 65$). These variables were also closely related to the variation in land surface temperature anomalies in the study area (range $R = 0.686$ – 0.791 ; $p < 0.0001$, $n = 65$). All thermal variables exhibited a significant positive trend between 1949 and 2013, both at the local (River Sella) and global (Northern Hemisphere and Europe) scales. There was also a significant increase in temperature anomalies in the period between 1986 and 1988 (Table 1, Fig. 2). For instance, the average anomalies in Europe (HadCRUT) changed from -0.02 °C (range, -0.29 – 0.24 °C) between 1950 and 1987, to 0.48 °C (range 0.08 – 0.74 °C) in 1988–2013. Average anomalies (E-OBS) in the study area increased from -0.06 °C (range -0.96 – 0.93 °C) in 1950–1986 to 0.56 °C (range -0.29 – 1.38 °C)

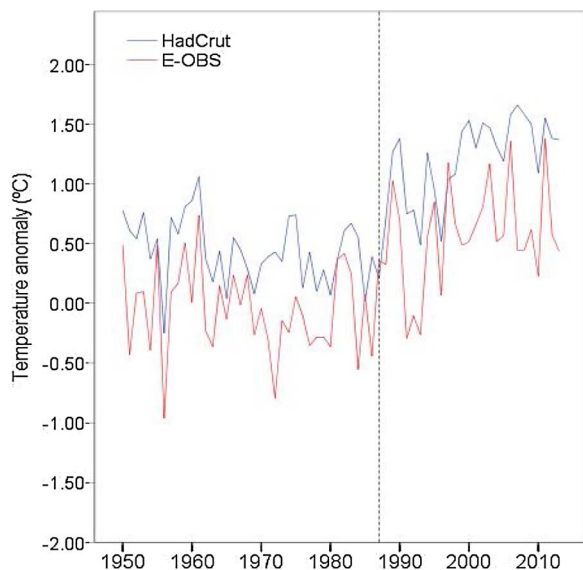


Fig. 2. Long-term changes in global (HadCRUT for Europe) and local (E-OBS) climate indicators from 1949 to 2013. The dashed line indicates the abrupt 1986–1988 shift in temperature anomalies mentioned in the text and in Table 1.

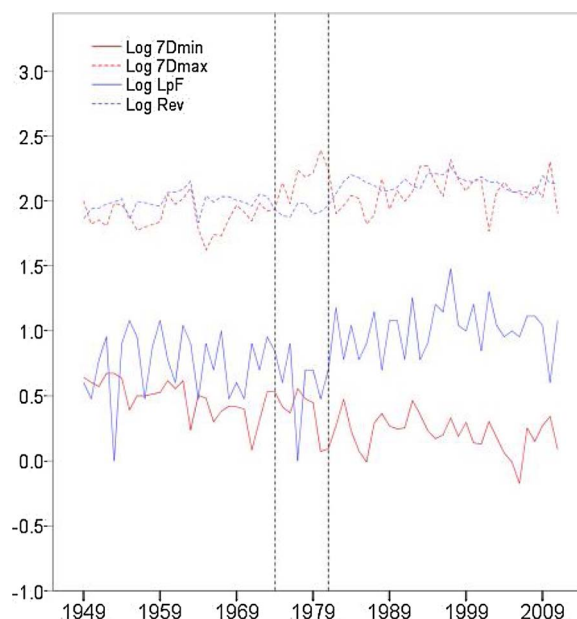


Fig. 3. Long-term changes in some hydrologic indicators of the River Sella from 1949 to 2013 (log transformed): maximum and minimum discharge during seven consecutive days (7Dmax, 7Dmin), annual frequency of low pulses (LpF), and annual number of reversals (Rev). The dashed lines indicate the period (1974–1981) when a significant shift was detected in the trend of hydrological variables (see Table 1).

in 1987–2013 (Fig. 2). The other climate variables revealed similar trends with a significant change in temperature anomalies in the 1980s.

Six of ten flow indicators showed a significant long-term trend. The maximum discharge during seven (7Dmax) and 30 consecutive days (30Dmax), the annual frequency of low pulses (LpF), and the annual number of reversals (Rev) increased significantly during the 65-year period. On the other hand, the minimum discharge during seven (7Dmin) and 30 consecutive days (30Dmin) decreased (Table 1, Fig. 3). Homogeneity tests showed an abrupt change in flow in the 1970s and early 1980s. This change was most apparent in the variables describing low flows. For example, average annual 7Dmin decreased by 47%, from $3.15 \text{ m}^3 \text{ s}^{-1}$ (range 1.21 – $4.71 \text{ m}^3 \text{ s}^{-1}$) in 1949–1979 to $1.68 \text{ m}^3 \text{ s}^{-1}$ (range 0.67 – $2.98 \text{ m}^3 \text{ s}^{-1}$) in 1980–2013. Likewise, average LpF increased by 83%, from 6 days a year (range, 1–12 days a year $^{-1}$) in 1950–1981 to 11 days a year (range, 4–30 days a year $^{-1}$) in 1982–2013 (Fig. 3).

Over the 65-year period considered, flow variations in the River Sella became extreme. There are scarce historical records of water temperature; but the available series from 1980 to 2011 correlated positively with the local temperature anomalies (E-OBS indicator; $R = 0.466$, $p = 0.007$, $n = 31$).

3.2. Salmon CPUE

Salmon CPUE decreased between 1949 and 2013 with a particularly strong decrease from 1973 to 1974 (Table 2, Fig. 4). There was a decline in the annual reported CPUE in the mid-1970s, from an average of 1377 fish (range 567–2871 fish) in the period 1949–1973 to 556 (range

Table 2

Values of parameters in the interrupted ARIMA (1,0,0) model (AR1, constant, intervention parameter Φ), standard error (SE) and t -test for time-series analyses of salmon CPUE (log) from 1949 to 2013 in the River Sella.

	B	SE	t-ratio	p
Constant	7.130	0.171	41.747	< 0.0001
AR1	0.373	0.119	3.138	0.003
Φ	−0.962	0.216	−4.463	< 0.0001

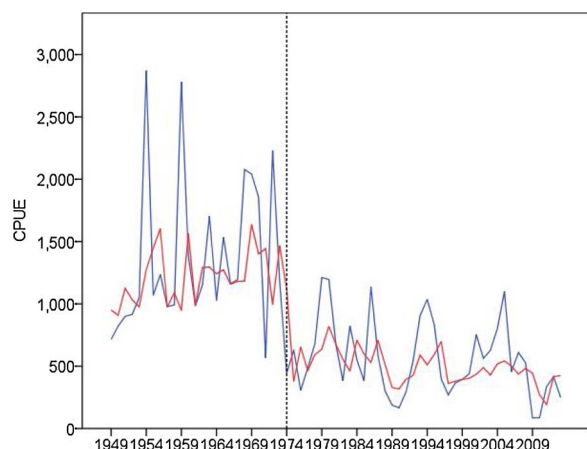


Fig. 4. Long-term changes in CPUE of Atlantic salmon in the River Sella from 1949 to 2013 (blue) in relation to predicted values (red) from the ARIMAX model after averaging the predictions of the best four models shown in Table 3. Prediction averaging was performed by means of the constrained least squares averaging scheme implemented in the *ForecastCombinations* R package (Raviv, 2015). The dashed line indicates the abrupt 1973–1974 shift in salmon catch mentioned in the text and in Table 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

85–1211 fish) in 1974–2013. Interrupted time-series analyses were therefore performed for 1949–1973 and 1974–2013.

The data series fitted a significant first-order vector interrupted ARIMA model (1,0,0) (Table 2). The intervention parameter (Φ) showed a significant downward trend in CPUE from the 1970s (Table 2). There was an abrupt and permanent (step) function (Fig. 4). After 1974 the number of returning salmon was ca. 550 fish. The residuals of the ARIMA model were not autocorrelated and normally distributed (Ljung-Box test, $\chi^2 = 13.122$, $p = 0.728$). The R^2 and normalized BIC of the model were 0.383 and 12.842, respectively.

Highly significant relationships were found between the salmon CPUE, and temperature and water flow indicators (Table 1). The number of returning adults declined as the temperature increased in both freshwater and marine habitats, and freshwater flow became extreme. The best ARIMAX models indicated however that the decrease in salmon CPUE was mainly driven by temperature trends (Table 3): besides the null model shown in Table 2, three competing models that included either local, global or both indicators of temperature anomalies were equally supported ($\Delta AIC < 2$; Burnham and Anderson 2002). This indicates that both local (temperature and flow in the river) and global (ocean temperature) factors have contributed to the decrease in salmon numbers and that temperature has played the major role.

4. Discussion

There was an abrupt decline in returning salmon in the 1970s, possibly triggered by overfishing at sea and a sudden outbreak of disease (Mills, 1989). The commercial salmon fishing around Greenland and the Faroe Islands, assumed feeding areas of Spanish salmon (Jacobsen et al., 2012; Reddin et al., 2012), crashed in the 1970s, and pre-fishery abundance declined by around 65% between 1975 and 2004 (Potter et al., 2004). Lack of Spanish salmon monitoring, limits the interpretation of these pressures. Concurrent with maximum fishing pressures in the ocean, there was an outbreak of ulcerative dermal necrosis (UDN, and secondary bacterial and fungal infections) on salmon in Spanish rivers in 1971 that caused high salmon mortality, especially in the River Sella (García de Leaniz and Martínez, 1988; Martín, 1988). Similar outbreaks of UDN were reported from the British Isles, France and Sweden around 1965–1975 (Munro, 1970; Roberts, 1993). Salmon diseases deserve special attention in a scenario of global warming, since their virulence may increase in a situation where the

Table 3

Interrupted ARIMAX (1,0,0) models fit to salmon CPUE (log) from 1949 to 2013 in the River Sella.

Model	$\Delta AICc$	BIC
AR1 + Φ + E-OBS	0.00	9.59
AR1 + Φ + GISS	0.12	9.71
AR1 + Φ	1.13	8.97
AR1 + Φ + GISS + E-OBS	1.89	13.15
AR1 + Φ + GISS + 7Dmax	2.16	13.42
AR1 + Φ + GISS + LpF	2.19	13.46
AR1 + Φ + E-OBS + 7Dmax	2.21	13.48
AR1 + Φ + E-OBS + LpF	2.22	13.49
AR1 + Φ + E-OBS + 7Dmin	2.32	13.58
AR1 + Φ + E-OBS + Rev	2.36	13.63
AR1 + Φ + GISS + 7Dmin	2.47	13.73
AR1 + Φ + GISS + Rev	2.54	13.81
AR1 + Φ + LpF	2.64	12.23
AR1 + Φ + 7Dmax	2.89	12.48
AR1 + Φ + Rev	3.37	12.96
AR1 + Φ + 7Dmin	3.49	13.08
AR1 + Φ + GISS + E-OBS + 7Dmax	4.16	17.01
AR1 + Φ + GISS + E-OBS + LpF	4.21	17.05
AR1 + Φ + GISS + E-OBS + 7Dmin	4.29	17.14
AR1 + Φ + GISS + E-OBS + Rev	4.39	17.23

Note: The models are ordered by $\Delta AICc$ value, which shows the difference between a model and the model with the lowest AICc. Only the 20 models with the lowest AICc are included. BIC values are also shown. AR1 is the first-order autoregressive term of the ARIMA (1,0,0) model, Φ is the intervention parameter, and the exogenous covariates are the local (E-OBS) and global (GISS) indicators of temperature anomalies and hydrologic alteration (7Dmin, 7Dmax, LpF, Rev).

fish are more stressed by high temperatures (Marcogliese, 2001; Miller et al., 2014). Despite a strong reduction in fishing pressure after the 1970s widespread collapse, our study population did not recover to previous abundance levels, which suggests the operation of additional factors.

From 1970 to 1980, flows in the study area became extreme and variable, especially during low flow events, whereas land-ocean temperature rapidly increased from the mid to the late 1980s, which was also apparent in air temperature at a local scale. In southern Europe, the anticipated effects of climate change in freshwater are a gradual warming and an increase in both the frequency and intensity of extreme events, such as floods and droughts (Rodó et al., 1997; Trigo et al., 2004; Lorenzo-Lacruz et al., 2012). Our findings confirm the existence of these two processes in the River Sella since the 1970s and 1980s. These local climate-mediated changes have probably influenced the life-history of salmon, with adverse consequences on the spawning stock size.

Three phases in the life cycle of salmon (juveniles in freshwaters, smolts in their first year at sea, and salmon growth at sea) appear especially vulnerable to climate change. Juveniles in fresh water are sensitive to high water temperatures. At temperatures above 18–20 °C, individual growth decreases (Ojanguren et al., 1999; Jonsson et al., 2001). At temperatures above 25 °C growth is negative and mortality increases concomitantly (Elliott and Elliott, 2010). Typically, salmon smolts migrate to sea in spring influenced by water temperature and flow (Otero et al., 2014). The migration starts earlier in a warmer climate, and increased water flow may also trigger the downstream migration of smolts in some rivers. On average, the outmigration has started 2.5 days earlier per decade during the last 50 years (Jonsson et al., 2016a,b). Extreme flows during autumn and winter can also initiate downstream displacements, although the young fish may not have the necessary physiological adaptations to regulate correctly their ion concentration in seawater, and survival can be low (Riley et al., 2008; Jonsson and Jonsson, 2014). In the River Sella, the growth rate of juveniles in freshwater and the age at smolting has decreased in recent decades (unpublished data), probably because of warmer water and flows that are more variable.

Post-smolt survival during the first weeks at sea strongly influence survival to adulthood (Friedland, 1998; Thorstad et al., 2012). Smolt survival at sea is also size-dependent, and sensitive to variable sea-surface temperature and food abundance and distribution (Beaugrand and Reid, 2003, 2012; Jonsson et al., 2016b; Jonsson and Jonsson, 2017). Jonsson and Jonsson (2009) suggested that smolt mortality might increase in a future climate due to an earlier migration from rivers, as has been observed in the River Sella and also elsewhere (Otero et al., 2014). In addition, ocean warming may affect the growth at sea and influence age at maturity (Todd et al., 2008; Jonsson et al., 2013, 2016a). This pattern has also been reported from east North American rivers (Friedland et al., 2005, 2009).

Climate influences animal lives not only by pervasive effects on metabolism and growth within the thermal niche, but also because of its function as timer influencing ecological decisions, such as when to out-migrate and when to return for reproduction (Hansen and Jonsson, 1991; Quinn et al., 2000; Waples et al., 2008; Valiente et al., 2011). Such traits are formed under intense selection influenced not the least in association with the life cycles of the important food organisms and predators in various parts of the habitat. For species, such as Atlantic salmon, assumed to migrate from Spain to feed at west Greenland and north of the Faroe Islands, conditions encountered in the nursery river are very different from those experienced by the juveniles and sub-adults in the ocean. Increased sea surface temperatures since the mid-1980s, together with changes in the pelagic food webs of the North Atlantic, are assumed to be main causes of increased marine mortality of Atlantic salmon (e.g. Friedland, 1998; Möllmann et al., 2005; Huusko and Hyvärinen, 2012). The progressive warming is associated with changes in composition, abundance and distribution of the planktonic crustaceans being key food items of salmon during the first year at sea (Jacobsen and Hansen, 2001; Beaugrand and Reid, 2003, 2012). Thus, climate change may not be synchronized over this vast area, and can cause mismatches between food supplies and other factors important for survival and growth, and evolved endogenous mechanisms formed by selection in the past in river and ocean.

The present climate change is rapid, and whether populations will be able to adapt depend on the inherent genetic variation in the gene pools. Thus, management should focus on maintaining the evolutionary potential within populations, in addition to conserving key habitats and minimizing additional stressors where possible, as a means to build resilience to ongoing climate change (Horreo et al., 2011; Reed et al., 2011). Evolutionary lines from the southern edge of the distribution area may be particularly important for managers, because of their long-term exposure to relatively high river temperatures.

Piou and Prévost (2013) assessed the impact of several climate factors on the persistence of the population and on the potential evolutionary dynamics, taking into account their phenotypic plasticity. Their findings showed that rising river temperatures over the next three decades could lead to an increase in smolt size that could benefit their survival at sea, thus increasing the population size. However, more of the juveniles may smolt younger (at age-1), and therefore not necessary larger (Jonsson et al., 2016b). Piou and Prévost (2013) agreed that changes in ocean conditions and an increase in flow amplitude are stressing pressures that act as counteracting factors and contribute to the risk of local extinction.

A possible loss of southern populations may imply a strong reduction in the genetic diversity of the species. To avoid extinction, extant populations may either find thermal refuges elsewhere (Dugdale et al., 2016) and/or adapt to warmer conditions. Anttila et al. (2014) demonstrated the plasticity of maximum cardiac performance of two Atlantic salmon populations within a northern and a southern European river, suggesting that this plasticity might aid salmon to cope with a warmer future. However, increased temperature during embryonic development influences later development, growth and life history traits (Finstad and Jonsson, 2012; Jonsson et al., 2014; Côte et al., 2016), with effects not easily foreseeable today.

5. Conclusions

As indicated by the present study, abundance of Atlantic salmon in southern Europe appears driven by both local and global factors, in which climate, as a determinant of flow and water temperature, plays a major role. Although commercial fishing pressure and outbreaks of diseases have diminished since the major decline in the 1970s, the population has not recovered and climate warming and changes in food webs of the North Atlantic are the most likely reasons. The future of the southernmost European populations is far from optimistic, since the environmental conditions are unfavourable to the species, and expected to worsen with future climate change. In the worst-case scenario, Atlantic salmon may disappear from these southern waters. To preserve the genetic diversity of the species, it is important to protect the old lineages, which currently consists of small populations surviving in unusual warm conditions at the extreme southern edge in Europe.

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